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DENTAL REMAINS OF EARLY BISON FROM THE TATROT FORMATION OF THE UPPER SIWALIKS, PAKISTAN

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ABSTRACT

Dental fossil remains assigned to cf. *Bison sivalensis* are described and discussed. The recovered assemblages comprising 3 upper molars and one lower premolar reflect the morphological features of the genus *Bison*. The discovered material comes from the late Pliocene continental deposits of the Tatrot village (Tatrot Formation, Upper Siwaliks, northern Pakistan) dated approximately from 3.3 to 2.6 Ma. A new finding for the site documents the dentition of the early bison.

Key words: Vertebrates, Mammals, Bovidae, Bovini, Bison, Siwaliks.

INTRODUCTION

The studied specimens came from the deposits nearby Tatrot village, Jhelum district, northern Pakistan (Fig. 1). The outcrops belong to the Tatrot Formation of the Upper Siwaliks (Shah, 1980; Johnson *et al*., 1982). The Upper Siwaliks fluvial sequence of the Indian subcontinent is one of the most continuous of its age, spanning in time from the Late Pliocene up to the Middle Pleistocene, ca. 3.3-0.6 Ma (Dennell *et al*., 2008; Behrensmeyer and Barry, 2005; Nanda, 2008). In the local lithostratigraphy the Upper Siwaliks comprises from the base to the top of the Tatrot Formation, the Pinjor Formation and the Boulder Conglomerate Formation (Nanda, 2002; Kumaravel *et al.,* 2005).

The fossiliferous deposits of the Tatrot Formation outcropping in the area consist of pale pinkish-orange brown clays, brownish grey siltstones and shale, and greenish grey fine to medium grained sandstones intercalated with dark grey conglomerates (Khan *et al*., 2010). Hussain *et al*. (1992) and Barry *et al*. (2002) dated the lower boundary of the Tatrot Formation between 3.5-3.3 or 3.4-3.2 My, corresponding to the lower part of the Gauss magnetochron, whereas Kumaravel *et al*. (2005), Dennell *et al*. (2008) and Nanda (2008) dated the upper boundary of the Tatrot Formation between 2.4-2.6 My. Thus, the Tatrot Formation roughly corresponds to the latest Pliocene. Apart from the specimens described here, fossil material attributed to proboscideans, artiodactyls, perissodactyls, primates and rodents (Colbert, 1935; Pilgrim, 1937, 1939; Sarwar, 1977; Akhtar, 1992; Nanda, 2002, 2008; Khan *et al*., 2009, 2010).

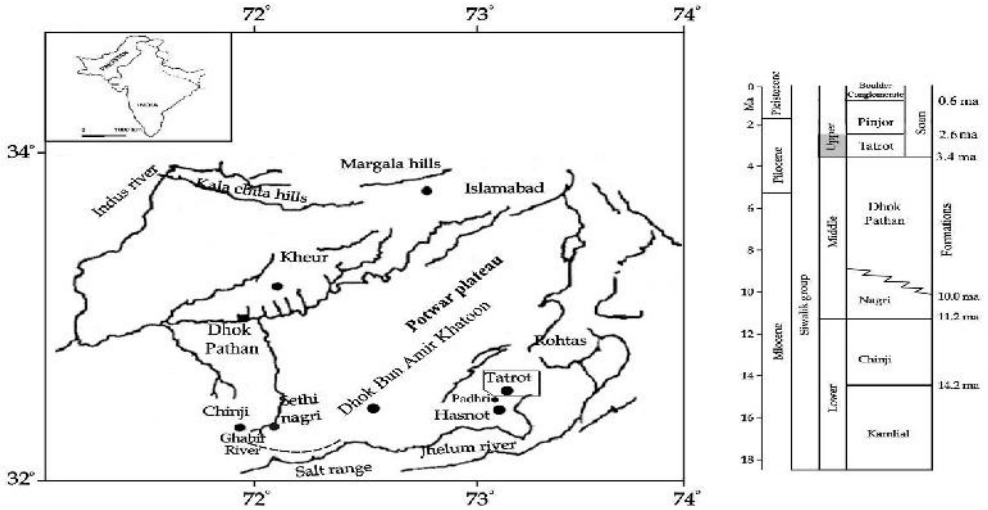

Figure 1: Map of the Potwar Plateau indicating the studied area and a generalized stratigraphic section of the main Siwalik formations (map is modified from Behrensmeyer and Barry 2005 and the boundary dates are from Dennell *et al*., 2008 and Nanda, 2008).

Abbreviations: PC-GCUF – Paleontological Collection of Government College University Faisalabad; PUPC – Punjab University Paleontological Collection; My – million years; m – molar; L – largest length; W – largest width; H – maximum height.

MATERIALS AND METHODS

All the specimens are collected by the surface collection method. Nevertheless, piercing instruments like chisel and geological hammers were employed for excavation of partially embedded fossils. Careful measures were taken so as to prevent the fossils from disintegrating during excavation. Each specimen was wrapped with a cotton piece to avoid the shocks of transportation. Eventually the collected specimens were brought in the laboratory for taxonomic and morphological analyses. Clay and other hardly adjoined sedimentary particles were removed with the help of fine needles and brushes. Accidentally broken fragments of specimens were rejoined by using gums and resins such as Magic Stone and Elfy. A hand lens was used for keen observation of very small and ambiguous morphological characters.

All the specimens are carefully observed for the description of morphological characters along with a discussion of their systematic determination. Measurements are taken with the help of a Vernier caliper and given in millimeters (mm). The catalogue number of the specimens consists of yearly and a serially catalogue number, so the number on the specimens represents the collection year (numerator) and the serial number (denominator) of that year (10/01). Uppercase letter with superscript stands for upper dentition and with subscript stands for lower dentition. The terminology of tooth crown elements and manners of measurements follow Gentry and Hooker (1988), and Gentry *et al.* (1999).

SYSTEMATICS

Family Bovidae Gray, 1821
Subfamily Bovinae Gray, 1821
Tribe Bovini Gray, 1821

Genus *Bison* Hamilton Smith, 1827

Type species: *Bison bison* (Linnaeus, 1758).

Generic diagnosis: Bovinae of large size; with frontal region not arched longitudinally, very broad in proportion to its length, which is less than the width between the orbits; face bent down on basicranial axisat an angle of about 30^{o} ; nasals short and broad; orbits prominent; horns implanted below the plane of occipital, far apart from one another, and situated not far behind the orbits, as in the *Bubalus,* diverging at their base at the angle of 180^{o}; short or long, curved forward and sometimes upward, slightly twisted clockwise; cross-section compressed to equilaterally triangular or cylindrical, keels more or less rounded or entirely absent, surface with deep longitudinal grooves; lacrymal with a narrow extention forward, in contact with nasals; premaxillae far removed from the nasals; parietal short and broad, only about one-sixth of the length of the frontal, inclined at a considerable angle to the plane of occipital, very nearly in the same plane as the frontal, and almost entirely developed on the roof of brain case, much overhanging the temporal fossae; temporal fossae very low, opening partly on to the parietal; occipital low in proportion to its breadth; auditory bulla large, much inflated; basiooccipital somewhat appoaching a quadrangular shape, posterior tuberosities not much expended laterally, surface flat or concave; palate but little extended behind the teeth, much thickened, especially in the median line; vomer not fused with palatine; teeth as in *Bubalus*, but upper molars rather more elongate with wide and complicated fossettes; entostyle very strong; enamel thick and moderately rugose; with abundant cement; styles and ribs very strong. Mandible moderately deep vertically and thick transversely; lower molars extremely hypsodont with distinct ectostylids; enamel thick and rugose; goat fold moderately developed; median ribs strong; stylids moderately developed. M_3 with large and stout heel with central inflated areas. P_4 and P_3 as in *Bubalus* but with distinct hypoconid; P_2 as in *Bos* but larger in size (Pilgrim, 1939).

Geographical distribution: The earliest geological record of *Bison* appears in the late Pliocene of China and Pakistan (Skinner and Kaisen, 1947; Akhtar, 1992; Khan *et al*., 2010). It is also known from the Pinjor stage of the Upper Siwaliks (Falconer, 1868; Lydekker, 1878; Pilgrim, 1939 and Akhtar, 1992). By the close of early Pleistocene, several species of *Bison* had reached the regions of Europe and Siberia, some of which crossed over to North America. The genus declined towards the late Pleistocene and at presents *Bison bonasus* is the sole survivor in Europe and *Bison bison* lives in North America (Bukhsianidze, 2005).

***Bison sivalensis* Lydekker, 1878**

Bos sivalensis Falconer, 1868 p. 555 [*nomen nudum*].
Bison sivalensis Lydekker, 1878 p. 122; pls. 15, 17, fig. 1.

Holotype. The partially preserved skull with registered number B 239 in the collections of the Geological Survey of India in Calcutta.

Diagnosis: A *Bison* with relatively high and narrow occipital region; frontals flat; parietals relatively well developed on the roof of brain-case; temporal fossae very narrow at their hinder ends, which are directed upward and inward, and indent the supraoccipital more deeply than in most other known species of *Bison;* horncores

relatively long, and curving upward and farward, anteroposteriorly compressed, cross-section with flat anterior surface, so that the anterior and inner keels, though well rounded, are distinguishable, posterior keel not indicated. Teeth as in *Bubalus* but upper molars rather more hypsodont with wide and complicated fossettes; entostyles strong and extendend transversely; enamel thick and rugose; styles and ribs very well developed (Pilgrim, 1939).

cf. *Bison sivalensis*

Material, locality and age: PC-GCUF 09/25 – partial right upper second molar (rM^2) collected from near Tatrot (Tatrot Formation); PUPC 07/154 – upper right third molar (rM^3) collected from near Tatrot (Tatrot Formation); PUPC 07/155 – upper left third molar (lM^3) collected from near Tatrot (Tatrot Formation); PUPC 99/87 – lower left fourth premolar (lP_4) collected from near Tatrot (Tatrot Formation). The Tatrot Formation approximately dated from ca. 3.4 to 2.6 My (Khan *et al*., 2010).

Description: PC-GCUF 09/25 is an isolated partial upper molar in an early wear (Fig. 2(1)). The enamel is fairly thick and moderately rugose. The entostyle is broken at its apex. The protocone appears to be more crescentic. The metacone is higher than the protocone. It is also higher than the hypocone which is slightly damaged at the apex. The curvature of the protocone is more acute than that of the hypocone. Its outer margin is slightly V-shaped. The anterior and posterior fossettes are equally wide and deep. A large spur (hypoconal spur) projects on the posterior side of the posterior fossette. A small spur also projects on the anterior side of the anterior fossette. The ribs are developed enclosing a furrow between them. The metastyle is strong while the mesostyle and the parastyle are missing. The molar is robust in general appearance. The distolingual enamel fold is present. The folded are prominent owing to mesiodistal compression. The posterior fossette has a long fold posteriorly. The comparative measurements are provided in table 1.

PUPC 07/154 and PUPC 07/155 are upper right and left third molars respectively (Figs. 2-3). The molars are extremely hypsodont, quaderate and in early wear (Table 1). The cement is well developed lingually and labially. The entostyle is completely exposed and clearly indicates that its thickness decreases with depth. The enamel is moderately thick and rugose all over the crown, particularly on the lingual side. The fossettes are narrow and deep. The anterior fossette is wider than the posterior one and unfolded. The posterior fossette has a long posterior fold. The preprotocrista gradually increases labially. The preprotocrista length is greater than the postprotocrista which is just touching the prehypocrista.The paracone is well developed and is larger than the metacone. The latter is comparatively higher than the former. Anteriorly the metacone is connected with the paracone and posteriorly it does not link with the hypocone. The hypocone is strongly crescentic with the longer and wider prehypocrista than the posthypocrista which is unworn. The median ribs are stronger than the styles. The median ribs produce vertical furrows against the styles.

PUPC 99/87 is a left lower premolar, hypsodont and in early wear (Fig. 4). The elongated metaconid takes an almost antero-posterior position directed to the rear and leaving a deep open anterior valley. The paraconid of the P_4 is strongly developed and rather larger than the parastylid. The entostylid is well developed and distinct from the entoconid. The metaconid is antero-posteriorly developed, especially, towards the crown's base, tending to close the anterior valley. The dentinal islet is present in the posterior valley of the premolar.

Table 1: Comparative measurements of the cheek teeth of cf. *Bison sivalensis*. * The studied specimens. Referred data are taken from Hay (1923), Akhtar (1992), Akhtar and Butt (1997) and Khan *et al*. (2010).

Taxa	Number	Nature/Position	Length	Width	W/L
cf. *B. sivalensis*	PC-GCUF 09/25*	rM^2	33.0	24.0	0.73
	PUPC 07/154*	rM^3	34.5	24.6	0.71
	PUPC 07/155*	lM^3	35.0	28.5	0.81
	PUPC 99/87*	lP_4	31.0	20.5	0.66
B. cf. *sivalensis*	PUPC 69/327	P_4	24.0	14.5	0.60
B. sivalensis	PUPC 95/26	M^2	36.0	32.0	0.88
	--	M^3	33.0	24.0	0.72
B. occidentalis	--	M^2	29.0	25.0	0.86
		lM^3	34.0	29.0	0.85
		rM^3	34.0	29.0	0.85
B. alleni		M^2	37.0	28.0	0.75
		lM^3	37.0	27.0	0.72
		lM^3	37.0	27.0	0.72
B. regius		M^2	39.0	32.0	0.82
		lM^3	46.0	36.0	0.78

Figure 2. cf. *Bison sivalensis*. **1**. PC-GCUF – rM^2. **2**. PUPC 07/154 – rM^3. **3**. PUPC 07/155 – lM^3. **4**. PUPC 99/87 – lP_4. a = occlusal view, b = lingual view, c = labial view. Scale bar 10 mm.

Comparison and Discussion: The studied teeth show typical bovid features. They are large and hypsodont. Broad upper molars are the characteristic of Bovinae and some genera (*Selenoportax*, *Pachyportax*) of Boselaphinae. Excessive antero–posterior compression of Bovini molars has produced median ribs of extraordinary strength. This type of development has also seen in Bopselaphini genera *Selenoportax* and *Pachyportax*

(Khan *et al*., 2009a). Nevertheless, Bovini teeth are characterized by extremely hypsodonty with cement, the disappearance of the wrinkles on the enamel and the enlargement of the entostyle and ectostylid (Pilgrim, 1939). The presence of the cement, the disappearance of the wrinkles on the enamel and the enlargement of the entostyle and excessive antero–posterior compression of the studied teeth confirm their inclusion to Bovini (Fig. 2). Furthermore, robust dental pattern associates the sample to bovines (Fig. 2).

In bovines the quadrate shape of the upper molars is a characteristic of *Proamphibos Hemibos, Proleptobos*, *Leptobos*, *Bos, Bison* and *Bubalus*. The less quadrate shape and more hypsodonty of the molars show affinities to the Taurina (*Bos*, *Leptobos*, *Bison*) rather than to the Bubalina (*Proamphibos Ampibos*, *Hemibos*) (Gentry, 1992). The studied teeth are hypsodont as in *Bubalis* and *Bison*. They are less hypsodont in *Proamphibos* and *Hemibos*. The molars differ from those of *Bubalis* in having a few projected folds in the fossettes. Unlike the studied sample, the posterior fossettes of *Bubalis* has a long posterior fold and generally an anterior one as well, which almost join one another (Pilgrim, 1947). This fold pattern is absent in the studied teeth. The studied teeth show similar morphological characters with those of *Bison*, in which distolingual fold is present in the upper molars (Martinez-Navarro *et al*., 2007). The lower P_4 has a distinct hypoconid which is the character of *Bison*. The dentition is comparable in size and proportions to that of *Bison sivalensis*, which is poorly known from the Siwaliks (Akhtar and Butt, 1997; Khan *et al*., 2010). Nevertheless, the dental characters do not really contribute to the taxonomic resolution precisely and consequently they are assigned to cf. *Bison sivalensis*.

The hypsodonty, size, round wearing cusps and occlusal complexity of the bison teeth described here all indicate some degree of reliance on dietary roughage, likely graze. These dental characters are today associated with herbivores present in dry and open environments (Kingdon, 1982). Janis (1982) already noted that Siwalik bovid show increases in size, hypsodonty and molarization, suggesting a move towards more fibrous diets and more open habitats. Studies demonstrating a strong negative relationship between hypsodonty and mean annual precipitation (Damuth *et al*., 2002; Fortelius *et al*., 2002, 2006), suggest that the high-crowned teeth of early Bovini are indicative of lessened rainfall and local environmental aridification in the Siwalik region at this time. Nevertheless, it is the larger-sized savanna species that are able to differentiate their diets the most, incorporating greater quantities of the taller, more fibrous, and less protein-rich grasses that remain in greater abundances during the dry season as suggested by Bell (1969).

Conclusions: The early bison *B. sivalensis* was recorded from the outcrops of the village Tatrot in the northern Pakistan. Nevertheless, Plio-Pleistocene Asian bisons are still poorly known. The finding of the early bison from the upper Pliocene deposits of the Upper Siwaliks is with the agreement of the previous concept (Khan *et al*., 2010). The early bison with the other inhabitants (elephants, horses, rhinoceroses, ruminants) of Tatrot indicates open woodlands and grasslands during the upper Pliocene.

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